

Variability of Barley Radiation-Use Efficiency

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ABSTRACT

Radiation-use efficiency (e) is a crop-dependent coefficient widely used in crop simulation models and in the physiological interpretation of crop response to the environment and management practices. Our objectives were to: (i) determine the e of spring barley (*Hordeum vulgare* L.), (ii) analyze the impact of weather variables and fraction of solar irradiance intercepted (f_i) on e , and (iii) compare reported estimates of e for barley and wheat (*Triticum aestivum* L.) with our measurements for barley. Field experiments were conducted in 2000 and 2001 at Pullman, WA. Treatments consisted of factorial combinations of two cultivars of spring barley (Baronesse and Steptoe), two seeding densities (250 and 100 plants m^{-2}), and two seeding dates (normal and late). Intercepted radiation was measured with tube solarimeters installed below the canopy during the crops life cycle and aboveground biomass obtained from weekly to biweekly samples. The extinction coefficient for solar radiation of both cultivars was 0.43, with no effect of seeding date and density. Cultivar, plant density, and f_i did not affect e ; however, e at the normal seeding date was greater than at the late seeding date in both years (1.15 and 1.19 g MJ^{-1} , first seeding date, and 0.90 and 0.95 g MJ^{-1} , second seeding date, Years 2000 and 2001, respectively, $P < 0.01$). These variations were correlated with daytime vapor pressure deficit (D). The e of barley and wheat reported in the literature and those obtained in this study were linearly related to D (kPa): $e = 1.88 - 0.53D$ ($r^2 = 0.70$, $n = 22$). Maximum values of e reported for barley and wheat are near 1.6 g MJ^{-1} , but our analysis suggests that these high values can only be achieved in low D environments. The effect of the evaporative demand of the atmosphere should be considered in the interpretation of measured e or in the use of e in crop simulation models.

THE CONCEPT of radiation-use efficiency (e) has been widely used in crop growth analyses. Warren Wilson (1967) introduced the relationship between crop growth rate and the amount of intercepted solar radiation as

$$C = e f_i S_i \quad [1]$$

where C is the rate of dry-matter production per unit ground area, S_i is the solar irradiance, f_i is the proportion of the radiation intercepted by vegetation, and e is the efficiency of use of intercepted radiation in dry-matter production. Knowing e and f_i , Eq. [1] offers a simple way of simulating crop growth. In summarizing published values of e , Warren Wilson (1967) recognized that it was reasonably constant for different crops. Monteith (1977) reported a linear relation between dry matter and intercepted radiation accumulation, with an average slope of 1.4 g MJ^{-1} for four C_3 crops growing under nonlimiting conditions. Monteith (1977) defined the slope as radiation-use efficiency and provided a theoretical basis

for the consistency of this relationship. Information on e for crops like corn (*Zea mays* L.) and wheat is abundant in the literature, but published values are scarce for barley (Sinclair and Muchow, 1999a).

The impact of physiological and environmental factors on e and its proper integration into crop simulation models remains debatable. Sinclair and Horie (1989) analyzed the theoretical link between nitrogen deficiencies and e for both C_3 and C_4 crops. They reported that e should decrease as nitrogen stress increases, and that the decrease should be closely linked to a decrease in leaf photosynthetic rate. At the field level, Gallagher and Biscoe (1978) found that e of fertilized wheat was 10% higher than e of nonfertilized wheat. In experiments with different nitrogen levels, e of wheat showed a curvilinear increase approaching asymptotically a maximum (Garcia et al., 1988; Fischer, 1993), in agreement with the theoretical considerations of Sinclair and Horie (1989). Similarly, water stress, which also decreases leaf photosynthetic rate, caused a decrease in barley e (Jamieson et al., 1995).

While the theoretical link between nitrogen or water deficiencies and e is well established and experimentally quantified, the effect of other factors on e of unstressed crops is still controversial (see Sinclair and Muchow, 1999b; Kiniry, 1999). There is some evidence that for well-watered crops, e decreases with an increase in the vapor pressure deficit of the air (D). Stöckle and Kiniry (1990) found that e based on intercepted photosynthetic active radiation (PAR) decreased with increasing D with a slope of -0.65 and -0.85 g MJ^{-1} kPa^{-1} for sorghum [*Sorghum bicolor* (L.) Moench] and corn, respectively. Manrique et al. (1991) found that slope to be -1.48 g MJ^{-1} kPa^{-1} for potato (*Solanum tuberosum* L.). This response may be due to an increase in the stomatal resistance with increasing D (Schulze and Hall, 1982; Dai et al., 1992), which in turn causes a decrease in the leaf photosynthetic rate as Bunce (2003) reported for potatoes and sorghum. Mott and Parkhurst (1991) concluded that stomata respond to the rate of transpiration rather than to humidity per se, a conclusion supported by Monteith (1995). Hence, the response of e to D can be seen as a particular case of the general response of e to an increment in the transpiration rate.

Theoretically, e should increase with a decrease in

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Abbreviations: C , rate of dry-matter production per unit ground area; D , vapor pressure deficit of the air; e , radiation-use efficiency; e_{aPAR} , e based on absorbed PAR; e_D , e adjusted by vapor pressure deficit; e_{ET_o} , e adjusted by ET_o ; $e_{i,solar}$, e based on intercepted solar radiation; $e_{i,PAR}$, e based on intercepted PAR; e_T , e adjusted by temperature; ET_o , reference crop evapotranspiration; f_{diff} , fraction of diffuse radiation; f_i , fraction of radiation intercepted by the canopy; f_T , temperature factor; HI, harvest index; k_s , extinction coefficient for solar radiation; PAI, plant area index; PAR, photosynthetic active radiation; S_i , solar irradiance; T , temperature; T_n , T_{op} , and T_x are minimum, optimum, and maximum temperature for photosynthesis.

the proportion of leaf area operating at saturating light level (Sinclair and Horié, 1989). This proportion depends on factors such as irradiance, fraction of diffuse to total radiation (f_{diff}), and plant area index (PAI). It is expected that e increases with a decrease in the irradiance and an increase in f_{diff} because in both cases the proportion of photosynthetic area that is operating at nonsaturating irradiance increases. These effects have been demonstrated by using simulation models (Allen et al., 1974; Norman and Arkebauer, 1991; Sinclair et al., 1992; Choudhury, 2000), and a small effect was documented in sunflower (*Helianthus annuus* L.) by artificially varying the radiation environment (Bange et al., 1997). Applying the same reasoning, an increase in f_i should increase e . In annual crops, this effect should be evident in the first stages of development, when the f_i (and PAI) is low. Gallagher and Biscoe (1978) first suggested this effect on barley and wheat, but it was explicitly studied by Trapani et al. (1992) on sunflower. They found a two-fold increase in e when the f_i of PAR was above 0.8 compared with canopies with f_i of PAR below 0.8. This result contrasts with the theoretical considerations of Sinclair and Horié (1989) and Choudhury (2000) on wheat that indicate that this effect is quantitatively marginal; the planophile habit and heliotropic behavior of sunflower leaves can perhaps explain the results of Trapani et al. (1992). Crop density could also affect e by altering f_i . Westgate et al. (1997) found no effect of density on e of maize, but Purcell et al. (2002) reported a decrease in e with increasing density in soybean. Whether f_i or plant density affect e of barley has not been analyzed.

Our objectives were to: (i) determine the e of spring barley, (ii) analyze the impact of weather variables and f_i on e , and (iii) compare reported estimates of e of barley and wheat with our measurements for barley.

MATERIALS AND METHODS

Field experiments were conducted in 2000 and 2001 at the Palouse Conservation Field Station (46°45'N, 117°12'W, elevation 756 m), located five km NW of Pullman, WA, on a Palouse silt loam (fine-silty, mixed, mesic Pachic Ultic Haploxerolls). The experimental area was surrounded by spring wheat. Treatments consisted of a factorial combination of two cultivars of spring barley (Baronesse and Steptoe), two seeding densities and two seeding dates, arranged in a complete randomized block design with four replications in 2000 and three replications in 2001. Each plot (2.2 by 12 m) was seeded with a no-till drill rows 20-cm apart. At seeding, each crop received 157 kg ha⁻¹ of nitrogen and 51 kg ha⁻¹ of phosphorus in the form of urea-ammonium nitrate and ammonium polyphosphate. Baronesse, a two-row barley, has a cycle about 1 wk longer and produces more tillers than Steptoe, a six-row barley. The seeding dates were 27 April and 6 June in 2000, and 26 April and 13 June in 2001. Target densities were 100 and 250 plants m⁻² but the average (range) obtained densities were 100 (70–113) and 190 (160–220) plants m⁻².

Gravimetric soil water content and bulk density (Year 2000) were measured at crop emergence to a depth of 1.8 m in 0.3-m increments. Plots were irrigated with sprinklers during the growing season to prevent water stress induced by soil water availability. Weeds were controlled by hand. Diseases and

insect damage were prevented or controlled with insecticides [chlorpyrifos: *O,O*-diethyl *O*-(3,5,6-trichloro-2-pyridinyl)phosphorothioate] and fungicides [propiconazole: \pm -cis-1-[2-(2,4-dichlorophenyl)-4-[(2-propynyloxy)methyl]-1,3-dioxolan-2-yl]-1*H*-imidazole monohydrochloride].

After the plants showed the tip of the fifth leaf in the main tiller, aboveground biomass and PAI were estimated from samples of two adjacent 0.5-m length rows (0.2 m²) per plot, at intervals of 6 to 10 d until physiological maturity. Samples were dried at 60°C for 72 h and the dry weight recorded. For each plot, a subsample of five plants was used to estimate the proportion of leaf, stem, spike and dead material of the sample. The area of each portion was measured with a leaf area meter (LI-3050A, LICOR Inc., Lincoln, NE), and the specific area of each portion calculated as the quotient between area and dry weight. Plant area index was calculated as the sum of leaf, stem and spike area indexes. At harvest, 2 m² of aboveground biomass was sampled, weighed (keeping subsamples to estimate moisture content) and threshed to evaluate yield, total aboveground biomass and harvest index (HI). No final harvest was possible in the second seeding date because of acute rodent damage after heading.

Radiation interception was measured with one tube solarimeter (70 cm) per plot (Marcos, 2000). After the plants reached the two to three-leaf stage, the solarimeters were placed below the canopy in areas representative of the plot. Each solarimeter was connected to a datalogger (CR10x, Campbell Scientific Inc., Logan, UT, USA), and the signal recorded every 20 min. Simultaneously, solar radiation was measured at a height of 2.5 m with a pyranometer (LI200X, LICOR Inc., Lincoln, NE, USA). The solarimeters were carefully leveled, regularly cleaned, and calibrated at the beginning and at the end of the growing season. The pyranometer and solarimeter outputs were integrated to obtain daily solar irradiance and daily solar radiation transmitted through the canopy, and the values used to calculate daily fractional and total radiation intercepted. During the first 25 (10) d after emergence of the first (second) seeding date in 2001, the solarimeters readings were scattered (Fig. 1b); the missing days were estimated by linear interpolation between actual measurements. Additionally, instantaneous measurements of intercepted PAR were obtained with a ceptometer (AccuPAR model PAR-80, Decagon, Pullman, WA). The fraction f_{diff} of the incoming radiation was estimated from the measured solar radiation and the expected solar irradiance for clear and overcast sky at Pullman calculated with the equations given by Campbell and Norman (1998, chapter 11). These equations give an estimate of beam and diffuse radiation in clear sky days; we further assumed that in completely overcast days all the radiation is diffuse. To calculate f_{diff} for a given day, we assumed that the diffuse component increases linearly and the beam component decreases linearly from clear to overcast sky.

Precipitation, temperature, relative humidity, and wind speed were recorded with a weather station located in the border of the experimental area. Sensors were at 1.5 m above the surface except the rain gage that was at 0.9-m height, and were connected to the same datalogger as the solarimeters and the pyranometer. Daytime D was calculated as the arithmetic mean of D values obtained when the pyranometer output was >1 W m⁻². To quantify the transpiration rate of an unstressed crop fully covering the soil, we calculated the reference crop evapotranspiration (ET_o) (Allen et al., 1998).

To explore differences in canopy architecture, we calculated the extinction coefficient for solar radiation (k_s) on the basis of the measured f_i and PAI solving k_s for the equation

$$f_i = 1 - \exp(-k_s \text{PAI}). \quad [2]$$

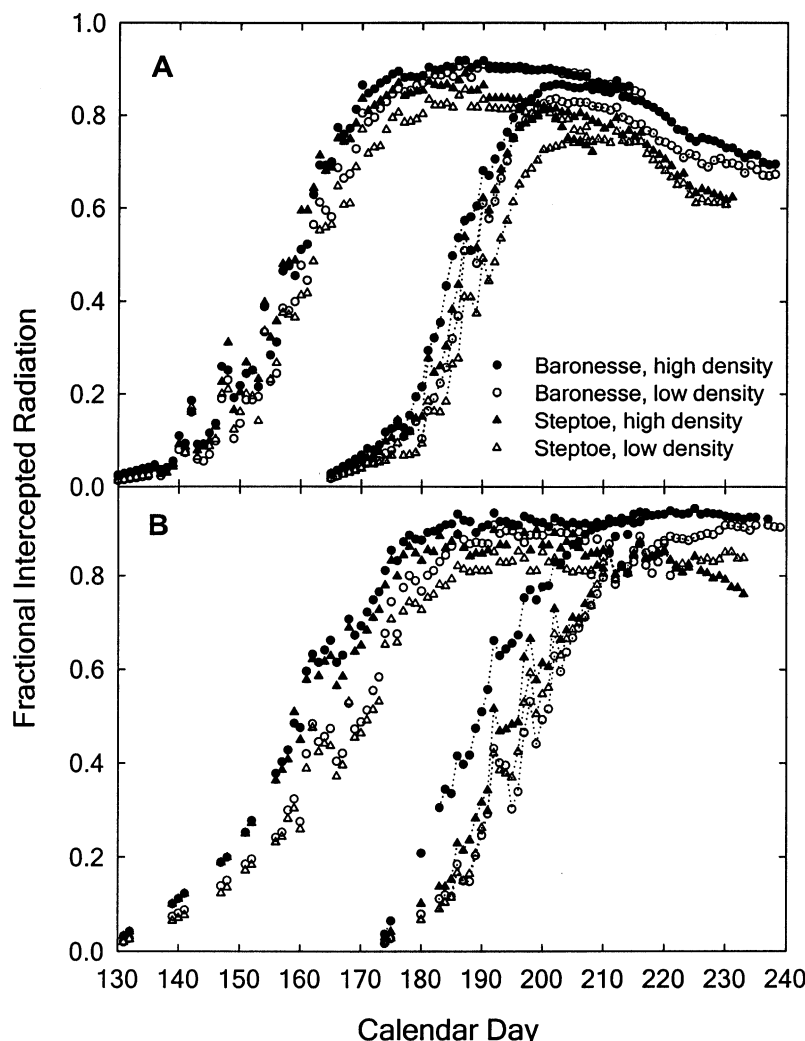


Fig. 1. Fractional solar radiation interception of two cultivars of spring barley (Baronesse and Steptoe) in two seeding dates in the Year 2000 (panel A) and 2001 (panel B). In 2000 (2001), each point is the average of four (three) replications. Crops emerged on Day 131 (131) and 164 (173) in 2000 (2001) for the first and the second seeding date (dotted line), respectively.

This is an empirical approach that encapsulates factors affecting radiation transmission, including changes in canopy architecture, f_{diff} , and solar elevation in the course of the growing season. Using a detailed model of canopy radiation transmission (unpublished), we found that changes in solar elevation cause k_s to vary <0.02 in the course of the growing season.

Radiation-use efficiency (e) was obtained as the slope of the linear regression between cumulative biomass and cumulative intercepted radiation. Differences in e were evaluated by the test of slopes described by Kleinbaum et al. (1998). Differences between treatments in yield, biomass, HI, and cumulative intercepted radiation were tested using analysis of variance (SAS Institute, 1999).

Literature Data

Data on e retrieved from the literature are based on intercepted solar radiation ($e_{\text{i-solar}}$), intercepted PAR ($e_{\text{i-PAR}}$) and absorbed PAR ($e_{\text{a-PAR}}$). To make the last two comparable with our measurements, conversion coefficients were obtained using methods discussed by Bonhomme (2000). This author remarked on common mistakes that appear in the literature when doing these conversions, and analyzed the variations on the conversion coefficients due to different radiation dynamics

(equatorial and temperate), PAI dynamics and canopy geometry. Criteria established to select e values from the literature were as follows. (i) Only studies with a solid description of the methodology used to determine intercepted or absorbed radiation by plant canopies were considered. Sinclair and Muchow (1999a) summarized common mistakes in calculating estimates of intercepted or absorbed radiation. (ii) Only data of unstressed crops were included. If the author(s) reported frost damage or nitrogen stress (e.g., Fischer, 1993), e values affected by these events were not considered. (iii) If point measurements of intercepted radiation were performed around noon (typically between 1000 and 1400 h), daily interception was probably underestimated, particularly at low PAI. To assess the degree of underestimation, we used a detailed model of canopy radiation interception (unpublished) with inputs of latitude, the reported range of PAI, and the calendar days during the experiment (e.g., Yunusa et al., 1993). (iv) If cultivar or nitrogen effects were compared, maximum values of e were selected unless the differences were not significant statistically or inconsistent for example across years. In that case, treatments were pooled and the e values recalculated (e.g., Major et al., 1988; Miralles and Slafer, 1997). (v) If the original regression of biomass vs. intercepted solar radiation was performed setting the intercept to zero, the regression was recal-

Table 1. Summary of meteorological conditions† during the experiments at Pullman WA, Years 2000 and 2001. The data brackets the period from emergence of the first seeding date to maturity of the second seeding date.

Calendar day	Maximum temperature		Minimum temperature		Solar radiation		Daytime vapor deficit		Precipitation + irrigation		ET _o ‡	
	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001
	°C				MJ day ⁻¹ m ⁻²		kPa		mm			
130	16.9	19.9	5.6	7.2	24.0	19.7	0.80	1.04	14	26	41.3	42.5
140	20.1	27.9	9.4	8.7	23.9	28.2	0.98	2.06	9	1	48.8	58.1
150	20.1	20.4	7.4	6.3	26.6	22.8	0.96	1.06	20	7	47.6	43.5
160	18.1	16.8	7.4	7.4	20.9	23.9	0.65	0.72	23	1	37.5	41.4
170	23.7	22.4	8.8	10.2	29.4	23.8	1.27	1.07	7	71	54.6	46.1
180	23.6	27.3	9.2	12.3	25.8	28.9	1.26	1.57	29	3	49.7	56.2
190	27.3	25.8	7.9	12.4	29.9	24.9	1.80	1.53	10	29	55.6	51.9
200	29.6	26.4	11.6	11.1	28.2	25.7	2.14	1.54	15	33	58.5	53.3
210	33.4	26.9	13.0	13.0	27.3	23.0	2.93	1.70	9	0	60.5	51.5
220	29.6	34.2	9.1	15.8	26.6	24.8	2.46	3.22	1	0	56.1	63.7
230	27.7	25.9	10.4	10.8	24.3	23.1	2.18	1.77	0	0	52.7	50.5
240		25.5		9.4		20.2		1.63		0		44.8

† Calendar day indicates the first of a 10-d interval. Temperature, radiation and vapor pressure deficit are averages; precipitation + irrigation and ET_o are cumulative.

‡ Reference evapotranspiration (Allen et al., 1998).

culated without that restriction whenever possible (e.g., Miralles and Slafer, 1997).

The methods used to estimate daytime D for the period in which e was measured depended on the data available. Ideally, hourly data of D is the best way of calculating daytime D . However, this information is seldom reported. On the basis of available data, estimations of D from the literature were derived using four different methods. (i) Where daily maximum and minimum temperature and relative humidity were available, daytime D was taken as 2/3 of the maximum daily D . Tanner and Sinclair (1983) used a coefficient between 2/3 and 3/4, and Stöckle et al. (1998) found that 2/3 accommodates very well information for several locations. Maximum D was assumed to coincide with time of maximum temperature and minimum relative humidity. (ii) Where daily maximum and minimum temperature were available, the dew point temperature was assumed to coincide with the minimum temperature with negligible variation through the day. Daytime D was calculated as 2/3 of the difference between vapor saturation at maximum and minimum temperature. (iii) Where only average temperature was available, estimates were transformed to (ii) by assuming a daily thermal amplitude based on location. For example, for Montevideo (Uruguay) and Buenos Aires (Argentina) with humid, temperate climate, the thermal amplitude during the period of growth of barley and wheat is between 8 and 10°C, while for a subhumid or Mediterranean environment like Pullman, WA, it is between 11 and 14°C. This method gives the weakest estimate of daytime D . (iv) When the mean daily D was available, the reported D was

converted to daytime D by multiplying by 1.2, a factor derived from data for Pullman, WA. For humid climates, this factor can be 1.1, but in summer it can be as high as 1.4. Tanner (1981) found that at Hancock Experimental Farm in central Wisconsin, the slope of the regression between the integrated D from 0900 to 1800 h for the period 1 June to 10 September (Years 1976–1978) and the mean of the D at minimum and maximum temperature (and approximation to the mean daily D) was 1.45 ± 0.16 .

RESULTS AND DISCUSSION

Growing Conditions

Average temperature was above 11°C for both years and seeding dates (Table 1) and did not limit crop growth (Major et al., 1988). The crops were well supplied with nitrogen and water, with exception of the first seeding date of 2000, where Baroness showed symptoms of mild water stress toward the end of the cycle due to failure of the irrigation system. For this crop, ET_o was 420 mm and the water supply (available water at emergence plus precipitation and irrigation) was 370 mm, causing a deficit of approximately 50 mm during grain filling.

Baroness produced greater biomass and intercepted more radiation than Steptoe (Table 2), probably due to its longer cycle. The biomass and HI of Baroness at

Table 2. Biomass, yield, harvest index (HI), and cumulative intercepted radiation† (CIR) in the first seeding date, Years 2000 and 2001.

		2000				2001				
Cultivar	df	Density	Biomass	Yield	HI	CIR	Biomass	Yield	HI	CIR
			g m ⁻²			MJ m ⁻²	g m ⁻²			MJ m ⁻²
Baronesse		low	1284	582	0.453	1394	1390	729	0.526	1279
		high	1284	607	0.472	1415	1419	779	0.549	1369
Steptoe		low	1086	571	0.523	1098	1033	582	0.562	1005
		high	1152	622	0.540	1200	1152	634	0.550	1185
Source of variation										
Cultivar (C)	1		*	NS	***	***	**	**	NS	***
Density (D)	1		NS	NS	*	NS	NS	NS	NS	***
C × D	1		NS	NS	NS	NS	NS	NS	NS	NS
CV, %			8.2	10.1	4.6	3.7	6.0	8.2	5.0	2.9

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† CIR is the integral through the season of the daily fractional interception times solar irradiance.

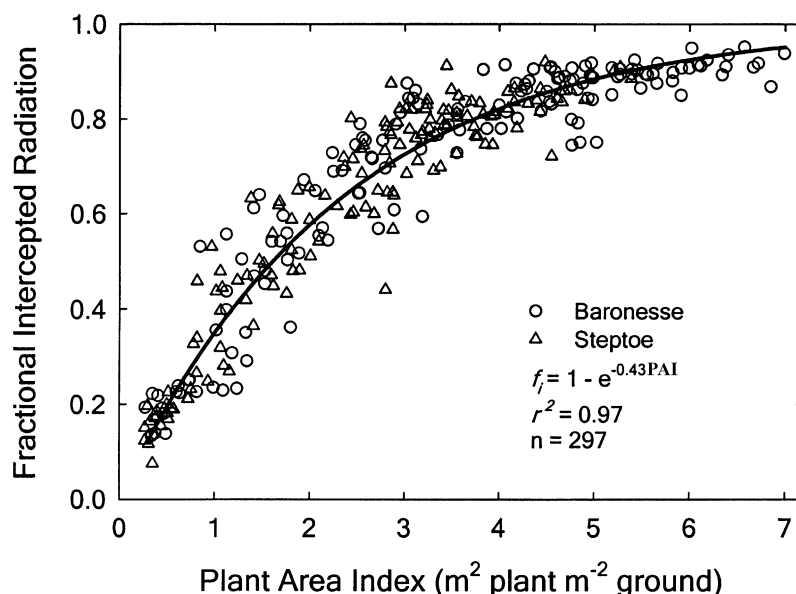


Fig. 2. Fractional solar radiation interception as a function of the plant area index (PAI) for the cultivars of spring barley Baronesse and Steptoe.

harvest were higher in the Year 2001 than in 2000, while for Steptoe they were similar in both years (Table 2). In addition, the nongrain portion of the biomass of Baronesse was similar in both years (690 ± 22 and $650 \pm 21 \text{ g m}^{-2}$ for the Years 2000 and 2001, respectively), but yield was 26% higher in 2001 than in 2000. These data provide evidence that Baronesse experienced water stress toward the end of the cycle in the Year 2000. Neither density nor the interactions were statistically significant for biomass, yield or HI in either year (Table 2).

Intercepted Radiation and Extinction Coefficient

The f_i was greater at high density in both years and seeding dates, although Baronesse at low density gradually achieved the same maximum interception as high density, particularly in the first seeding date (Fig. 1). This is due to the vigorous tillering of this cultivar, which produced a maximum of 12.0 ± 0.7 tillers plant^{-1} at low density, and 6.9 ± 0.7 tillers plant^{-1} at high density. In contrast, low density of Steptoe had the lowest f_i throughout the growing season in both years and seeding dates (Fig. 1); this cultivar produced a maximum of 7.7 ± 0.7 tillers plant^{-1} at low density, and 5.1 ± 0.5 tillers plant^{-1} at high density. The cumulative interception at high density was 5 and 11% greater than at low

density for the Years 2000 and 2001, respectively, but statistically significant only in the Year 2001 (Table 2). The low density approached the same interception as the high density treatment because of the proportionally greater contribution to the standing biomass of secondary tillers, which determined a delay of physiological maturity of 2 to 6 d, particularly in Baronesse.

The f_i was strongly related to PAI (Fig. 2). The estimated k_s ranged from 0.40 to 0.52, both extremes occurring in the second seeding date of 2001 (Table 3). Within year and seeding date, the k_s tended to be higher at low density but the difference was significant only in the second seeding date of 2001 (Table 3). When the k_s of each density was calculated pooling year and seeding date, the difference was statistically significant (0.45 ± 0.01 vs. 0.42 ± 0.01 , $P < 0.002$). It suggests that at low density the canopy adjusted slightly its structure to intercept more radiation. Genotypic differences in canopy architecture were also reflected in attenuation of solar radiation. Within year and seeding date, the k_s of Steptoe tended to be higher than the k_s of Baronesse, but the difference was not statistically significant (Table 3). When the k_s of each cultivar was calculated pooling year and seeding date, the k_s of Steptoe was statistically greater than the k_s of Baronesse (0.44 ± 0.01 vs. $0.42 \pm$

Table 3. Extinction coefficient for solar radiation ($k_s \pm \text{SE}$) and radiation-use efficiency ($e \pm \text{SE}$) for two cultivars of spring barley (Baronesse and Steptoe) at two densities in two seeding dates in the Years 2000 and 2001.

Year	Seeding date	Density	k_s		e	
			Baronesse†	Steptoe	Baronesse	Steptoe
g MJ ⁻¹						
2000	normal	low	0.43 ± 0.01	0.46 ± 0.02	1.12 ± 0.03	1.18 ± 0.04
		high	0.42 ± 0.01	0.43 ± 0.01	1.16 ± 0.04	1.14 ± 0.05
	late	low	0.47 ± 0.02	0.44 ± 0.02	0.85 ± 0.05	0.95 ± 0.07
		high	0.43 ± 0.01	0.44 ± 0.01	0.87 ± 0.07	0.97 ± 0.03
2001	normal	low	0.41 ± 0.02	0.47 ± 0.03	1.14 ± 0.07	1.10 ± 0.07
		high	0.41 ± 0.02	0.42 ± 0.02	1.22 ± 0.06	1.31 ± 0.08
	late	low	0.52 ± 0.03 a	0.51 ± 0.03 a	0.96 ± 0.08	1.03 ± 0.08
		high	0.40 ± 0.02 b	0.44 ± 0.02 b	0.99 ± 0.07	0.87 ± 0.06

† Within year and seeding date, different letters indicate significant differences between density x cultivar treatments at $P < 0.05$.

0.01, $P < 0.03$). Both the effects of density and cultivar on k_s were small, and a single k_s of 0.431 ± 0.004 ($r^2 = 0.97$, $n = 296$) provided a good fit for all data (Fig. 2). This value is in the lower end of the range of 0.41 to 0.58 given by Yunusa et al. (1993) for three spring wheat cultivars and in the upper end of the range of 0.28 to 0.44 given by Green (1989) for five cultivars of winter wheat. This indicates that in comparing barley and wheat, differences in architecture are associated more with variation among cultivars within a species than with variation among species.

Radiation-Use Efficiency

Biomass and cumulative intercepted radiation were linearly related (Fig. 3). To obtain the e coefficients, data of intercepted radiation and biomass at harvest were removed from the regressions because they consistently fell below the regression line, indicating a sharp decrease in e at the end of the cycle, particularly at high density (Fig. 3a and 3c). This result was expected since at that stage the crops had entered accelerated senescence and part of the interception was increasingly attributable to yellowing spikes and stems. Also, as mentioned above, Baronesse suffered a moderate terminal water stress in the first seeding date of the Year 2000 that limited the growth in the last two weeks of the cycle. Within year and seeding date, neither density nor cultivar affected e of barley significantly (Table 3). There was a weak tendency of the high density to have higher e in the first seeding date of the Year 2001 in the first seeding date (Table 3); pooling the data across cultivars, the e at high and low density were 1.23 ± 0.07

and $1.13 \pm 0.05 \text{ g MJ}^{-1}$ respectively, but the difference was not significant ($P < 0.11$). This small difference seems to be unrelated to differences in f_i or PAI achieved at different densities. Although in the early growth f_i was lower at low than at high density, the difference decreased as the season advanced, particularly in Baronesse (Fig. 2). Moreover, the difference in f_i was substantial only between Steptoe at low density and Baronesse at high density after flowering, when f_i was above 0.8 (Fig. 1). At this level of interception, which corresponds to $\text{PAI} > 4$, it is unexpected that the canopy photosynthesis will operate at saturating level. The sunlit PAI for a canopy with spherical leaf angle distribution would be around 1.4 if $\text{PAI} > 3$. This implies that for $\text{PAI} = 4$, less than 35% of the leaf area is eventually operating at saturating light level. Hence, plant density had an insignificant effect on e under the conditions of this experiment.

Although Baronesse and Steptoe are visually easy to distinguish, their canopy geometries as evaluated by k_s were almost identical. Differences in e were also negligible; therefore, greater biomass in Baronesse can be attributed to a longer cycle and greater cumulative intercepted radiation than Steptoe (Table 1). Since these two cultivars are high yielding in eastern Washington, it would suggest that both have optimized the e attainable in this environment and that further increase in the biomass production under unstressed conditions would depend on intercepting more radiation.

Data of biomass and cumulative radiation interception were pooled to obtain single values of e per year and seeding date (Fig. 3). Radiation-use efficiency remained

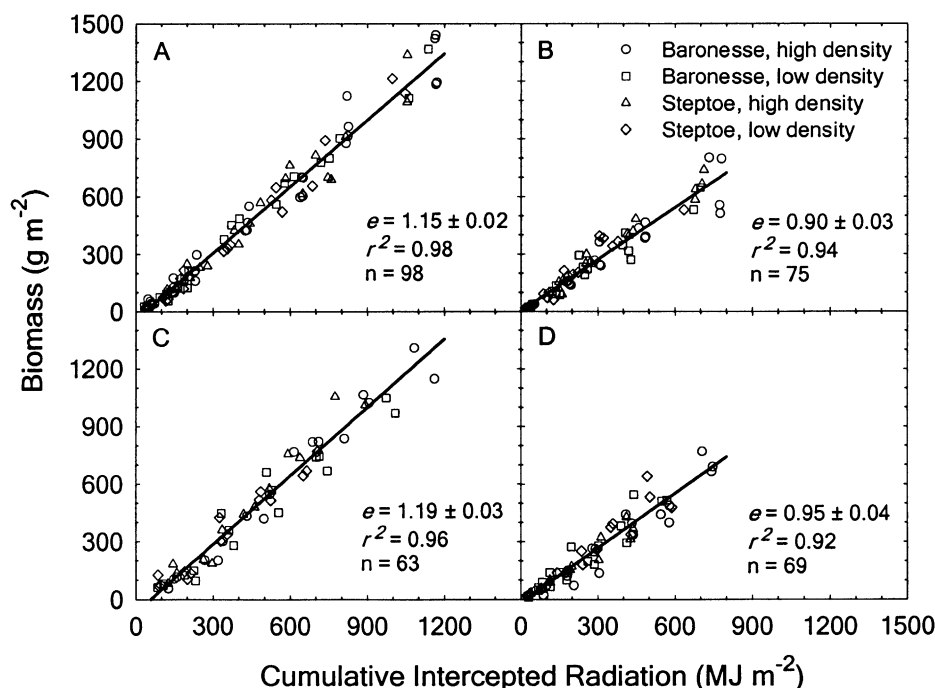


Fig. 3. Cumulative biomass as a function of the intercepted solar radiation of two cultivars of spring barley (Baronesse and Steptoe) at two densities in two years (2000 panels A and B, 2001 panels C and D) and seeding dates (first seeding date panels A and C, second seeding date panels B and D). The slope of the relationship between the two variables is the radiation-use efficiency (e). Flowering occurred when crops reached biomass levels between 400 and 550 g m^{-2} .

Table 4. Correlation coefficient between radiation-use efficiency (e) of spring barley, maximum (T_{\max}), minimum (T_{\min}), and average temperature (T_{avg}), average solar radiation (S_t), fraction of diffuse radiation (f_{diff}), daytime vapor pressure deficit (D) and average daily reference evapotranspiration (ET_o), for spring barley in two years and two seeding dates. Data were averaged over the same time interval used to calculate e . Each correlation coefficient was calculated with four pairs of data corresponding to normal and late seeding date for the Years 2000 and 2001.

	T_{\max}	T_{\min}	T_{avg}	S_t	f_{diff}	D	ET_o
e	−0.985*	−0.480	−0.922	−0.264	0.554	−0.955*	−0.950*
T_{\max}		0.441	0.915	0.353	−0.616	0.986*	0.973*
T_{\min}			0.767	−0.659	0.431	0.289	0.220
T_{avg}				−0.041	−0.249	0.837	0.797
S_t					−0.950*	0.506	0.552
f_{diff}						−0.739	−0.780
D							0.996**

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

constant from early tillering to well within grain filling (Fig. 3). This contrasts with the results of Calderini et al. (1997) and Foulkes et al. (2001), who found a decrease in e after anthesis in wheat. Since developing seeds are sinks for nitrogen, it is arguable that if the source of that nitrogen is the foliage, then a decrease in e should be expected due to a decrease in the photosynthetic capacity of the canopy. In our experiments, the nitrogen status of the crops was above sufficiency levels during the entire crop life cycle (data not shown), which could delay the translocation of nitrogen from the leaves to the grains. Another reason to expect a decrease in e after anthesis is the interception of radiation by reproductive structures on top of the canopy. We measured PAR interception by the spikes of Baronesse and found that they can intercept 30 to 40% of incident PAR (crops with approximately 800 spikes m^{-2} , data not shown), suggesting that (i) the spikes contribute significantly to canopy photosynthesis, possible through photosynthesis by awns (Blum, 1985), or (ii) the fraction of radiation transmitted through the spike layer to the leaves is used with higher efficiency (higher e) than the direct radiation. This higher efficiency could be explained by an increase in the proportion of diffuse radiation because of the scattering produced by the spikes. We can speculate, however, that e before heading was underestimated because we did not account for the roots, which can be a major sink for carbon during the preanthesis growth of cereals (Gregory et al., 1978). Constancy of e through the growing cycle provides a useful tool to model above-ground accumulation on the basis of Eq. [1].

A test of slopes for the four resulting e (two years and two seeding dates) indicated that the early seeding date had higher e than the late seeding date in both years. The maximum e estimated in these experiments was 1.19 g MJ^{-1} . We explored the relationship between envi-

ronmental variables and e by correlation analysis. Radiation-use efficiency correlated negatively with maximum temperature (range $23.2\text{--}28.0^\circ\text{C}$) and daytime D (range $1.2\text{--}1.9 \text{ kPa}$), but not with solar radiation (range $24.5\text{--}27.8 \text{ MJ day}^{-1}$) or f_{diff} (range $0.18\text{--}0.22$). Maximum temperature and daytime D correlated positively (Table 4). Goynes et al. (1993) also found no correlation between e of barley and incident radiation, but a negative correlation between e and D ; however, they did not report the slope of the relationship. If, as discussed in the introduction, the response of e to D is a particular case of the general response of e to the transpiration rate, we can expect a negative correlation between e and ET_o . We found these variables to be negatively correlated (Table 5). An advantage of this relation over the relation between e and D would be that ET_o combines in a biophysically sound manner the effect of solar radiation and temperature, which were observed to correlate with e in potato (Manrique et al., 1991).

The correlation between daytime D and maximum temperature highlights the difficulty in separating the potential depressing effect of these variables on photosynthesis and hence on e . By keeping the leaf-to-air $D < 1 \text{ kPa}$, Kobza and Edwards (1987) showed that wheat photosynthesis decreased sharply as temperature increased above 30°C . Leach (1979) measured wheat photosynthesis at constant 25°C air temperature and varying D and found the leaf photosynthesis was insensitive to D for $D < 1 \text{ kPa}$ but decreases for $D > 1 \text{ kPa}$. Therefore, even at optimum temperatures, the photosynthetic rate could be limited by $D > 1 \text{ kPa}$; at air temperature of 25°C and a dew point temperature of 10°C as is often the case at Pullman (Table 1), D is almost 2 kPa . In an attempt to separate any confounding effect of maximum temperature, D , and ET_o , we recalculated the cumulative intercepted radiation on an hourly basis weighing

Table 5. Radiation-use efficiency (e) of two cultivars of spring barley (Baronesse and Steptoe) obtained by adjusting the hourly cumulative intercepted radiation by temperature (e_t), air vapor pressure deficit (e_D), and reference evapotranspiration (e_{ET}), for two seeding dates (normal and late), Years 2000 and 2001. See text for explanations.

	2000		2001	
	Normal†	Late	Normal	Late
e , g MJ^{-1}	$1.15 \pm 0.02a$	$0.90 \pm 0.03b$	$1.19 \pm 0.03a$	$0.95 \pm 0.04b$
e_t , g MJ^{-1}	$1.25 \pm 0.02a$	$0.96 \pm 0.03b$	$1.28 \pm 0.04a$	$1.00 \pm 0.04b$
e_D , $\text{g MJ}^{-1} \text{ kPa}^{-1}$	1.73 ± 0.03	1.84 ± 0.06	1.83 ± 0.06	1.64 ± 0.06
e_{ET} , $\text{g} \times 10^{-1} \text{ MJ}^{-1} \text{ mm}^{-1}$	$3.26 \pm 0.06a$	$2.80 \pm 0.09b$	$2.89 \pm 0.09b$	$2.43 \pm 0.09c$

† Within rows, different letters indicate significant differences between year \times seeding date at $P < 0.05$.

the effect of temperature, D and ET_0 . Then, we obtained new expressions of e as the slope of the linear relation between cumulative biomass and adjusted intercepted cumulative radiation. To weight the effect of temperature on photosynthesis, the hourly radiation intercepted was multiplied by a temperature factor f_T that varies from 0 to 1, obtained from the following function adapted from Thornley (1998, chapter 3):

$$f_T = (T - T_n)^q (T_x - T)(T_{op} - T_n)^{-q} (T_x - T_{op})^{-1} \quad \text{for } T_n < T < T_x; \\ T_{op} = (T_n + qT_x)(1 + q)^{-1}, \quad [3]$$

where T is the hourly air temperature, T_n and T_x are the minimum and maximum temperature for photosynthesis, q is a parameter that determines the shape of the equation, and T_{op} is the temperature at which photosynthesis is maximum. By surveying literature data we found that $T_n = 0^\circ\text{C}$, $T_x = 45^\circ\text{C}$, and $q = 1.2$ (implying that $T_{op} = 24.5^\circ\text{C}$) provide a reasonable response for C_3 crops of cool season (Fig. 4).

To weight the effect of D on photosynthesis, the hourly intercepted radiation was divided by the hourly value of D . However, the occurrence of hours of very low D yielded a curvilinear relationship between cumulative biomass and this newly calculated cumulative intercepted radiation. Hence, on the basis of the results of Leach (1979), we assumed that photosynthesis was insensitive to D for $D < 1$ kPa and D was set to 1 kPa if $D < 1$ kPa. To weight the effect of ET_0 , we followed a similar approach, dividing the hourly intercepted radiation by the hourly ET_0 .

The temperature adjustment had an insignificant effect on e (Table 5). The relative ranking of e was identical to the one obtained by calculating e using cumulative intercepted radiation without any adjustment. The adjustment by D removed any significant differences between e (Table 5) and strongly suggests that the cause of the decrease in e in the late seeding date compared

with the normal seeding is the increase in D . The adjustment of e by ET_0 yielded significant differences between the e values (Table 5), indicating that the correlation between e and ET_0 (Table 4) is a consequence of the correlation between ET_0 and D . That normalization of the intercepted radiation did not account for the effect of seeding date and year on e , weakening the argument that the mechanism accounting for the effect of D on e is the increase in the transpiration rate. However, in the calculation of ET_0 the canopy resistance to vapor flux is by convention left constant, even though there is evidence that leaf and canopy resistance to vapor flux increase with increasing D (Schulze and Hall, 1982; Dai et al., 1992).

To further explore the relationship between e and D for barley, we gathered information on e for barley and wheat (under the assumption that these species have similar e) and estimated the average daytime D (Table 6). Values of e based on intercepted or absorbed PAR reported in the literature were converted to intercepted solar radiation (Table 6). A plot of e vs. daytime D is presented as Fig. 5. There is a tendency of e to decrease with increasing D as observed for other crops; barley and wheat seem to have the same response and were pooled in the regression. The slope of the relationship between e and D was $0.53 \pm 0.08 \text{ g MJ}^{-1} \text{ kPa}^{-1}$. The jackknife residuals used to test the presence of outliers (Kleinbaum et al. (1998), p. 228) indicated that one observation corresponding to Miralles and Slafer (1997) could be regarded as an outlier. The authors did not discuss possible reasons for such results, but it was anomalous compared with e of other treatments reported in that paper and consequently it was not included in the regression.

The slope of the regression is not directly comparable with the slope presented by Manrique et al. (1991) for potatoes because they expressed e based on intercepted PAR (with PAR being 0.45 of total incident radiation)

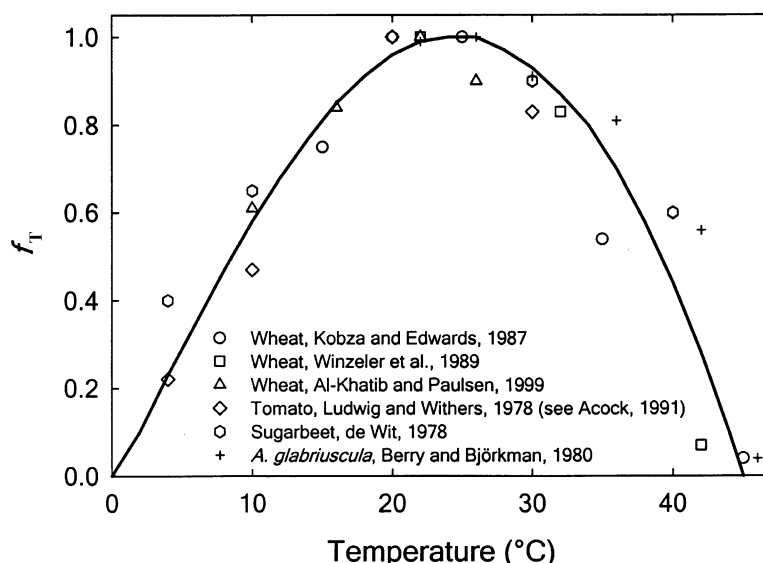


Fig. 4. Temperature dependence of photosynthesis for the C_3 species wheat, tomato (*Lycopersicon esculentum* Mill.), sugarbeet (*Beta vulgaris* L.) and *Atriplex glabriuscula* Edmonston. The line represents the temperature factor (f_T) as presented in Eq. [3].

Table 6. Summary of e retrieved from the literature (e_{a-PAR} = based on absorbed PAR, e_{i-PAR} = based on intercepted PAR) and their conversion to e based on intercepted solar radiation ($e_{i-solar}$), and the corresponding estimates of daytime vapor pressure deficit (D). See text for details on the method to estimate daytime D (Met. case).

Source	Location	Variables	Reported e	Reported or estimated $e_{i-solar}$	Met. case	Estimated daytime D	Comments
			g MJ^{-1}			kPa	
Goynes et al., 1993	Queensland, Australia	cultivar, year	e_{a-PAR} 2.90 ± 0.10	1.54	4	0.66	barley cv. Gilbert, 1990
Abatte et al., 1997	Balcarce, Argentina		e_{i-PAR} 2.70 ± 0.11	1.49	3	0.81	wheat, average temperature 16.7°C, assumed thermal amplitude 10°C
Miralles and Slafer, 1997	Buenos Aires, Argentina	isolines of different height, year, seeding date		0.98 ± 0.06 1.55 ± 0.14 1.25 ± 0.14 1.28 ± 0.06	2	0.76 0.71 0.79 0.95	wheat, average of standard height and semidwarf isolines. In order, 1st and 2nd seeding date for 1991 and 1992.
Fischer, 1993	New S. Wales, Australia	nitrogen	e_{a-PAR} 2.86 ± 0.14	1.47	3	0.68	wheat, average temperature 13.4°C, assumed thermal amplitude 10°C
Yunusa et al., 1993	Perth, Australia	cultivar, year	e_{i-PAR} 2.93 ± 0.17	1.69	2	0.66	wheat, cv. Kulin, year 1990
Major et al., 1992†	Lethbridge, Canada	cultivar, irrigation, year	e_{a-PAR} 2.42 e_{a-PAR} 2.45 e_{a-PAR} 2.25 e_{a-PAR} 2.48 e_{a-PAR} 2.51 e_{a-PAR} 2.31 e_{a-PAR} 2.63 e_{a-PAR} 3.06	1.25 1.27 1.17 1.28 1.30 1.20 1.36 1.58	1	1.19 1.19 1.19 1.19 1.22 1.22 1.22 1.22	soft white spring wheat, 1989 (two cultivars) spring wheat, 1989 (two cultivars) hard red spring wheat, cv. Neepawa, 1989 durum wheat, cv. Kyle, 1989 soft white spring wheat, 1990 (two cultivars) canadian prairie spring wheat, 1990 (two cultivars) hard red spring wheat, cv. Neepawa, 1990 durum wheat, cv. Kyle, 1990
Foulkes et al., 2001	Nottinghamshire, UK	cultivar, year		1.60	3	0.65	winter wheat, preanthesis period, 1994 and 1995 (six cultivars)
Unpublished	Pullman, WA, USA			1.07 ± 0.04 1.24 ± 0.03	1	1.31 1.00	wheat, cv. Hank, year 2001 wheat, cv. Falcon, year 2002

† Data of the year 1988 were excluded because biomass was probably underestimated. The reported harvest index for that year was near 0.6, while for the other years it was <0.4.

and D as daily mean instead of daytime average. Following the methodology used by Manrique et al. (1991) we converted e from PAR to solar radiation based by multiplying their reported e by 0.54. To convert daily mean to daytime D we multiply the former by 1.2 (see Materials Methods). With these factors, the slope recalculated for potatoes is $0.67 \pm 0.15 \text{ g MJ}^{-1} \text{ kPa}^{-1}$ ($r^2 = 0.63$, $n = 13$), and is indistinguishable from the slope of $0.53 \pm 0.08 \text{ g MJ}^{-1} \text{ kPa}^{-1}$ obtained for barley and wheat,

indicating a similar sensitivity of e to D for these crops. Applying the same calculations to the slopes of -0.85 and $-0.65 \text{ g MJ}^{-1} \text{ kPa}^{-1}$ reported for corn and sorghum by Stöckle and Kiniry (1990), we obtained slopes of 0.30 ± 0.12 ($r^2 = 0.50$, $n = 8$) and 0.40 ± 0.08 ($r^2 = 0.76$, $n = 9$) $\text{g MJ}^{-1} \text{ kPa}^{-1}$ for corn and sorghum, respectively. This suggests that the two C_4 species have less sensitivity to the effect of D than C_3 species. Morison and Gifford (1983) found that the decrease in stomatal

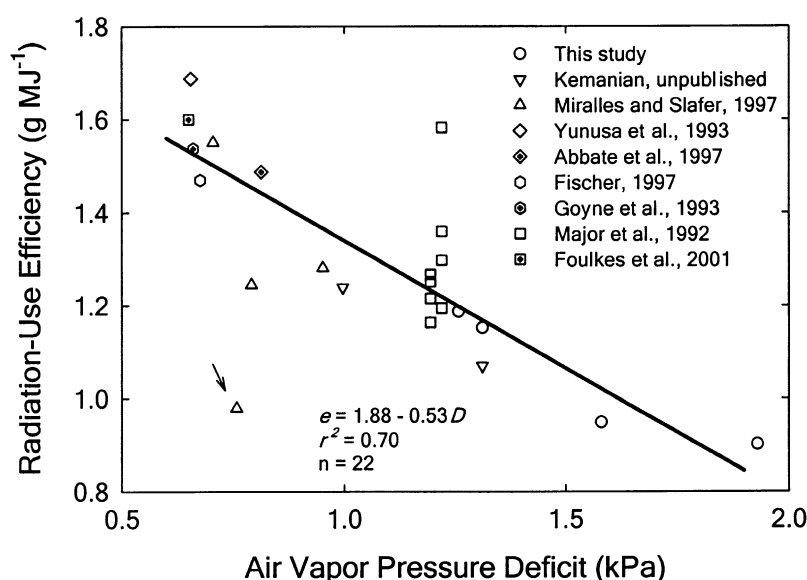


Fig. 5. Radiation-efficiency (e) as a function of the daytime vapor pressure deficit of the air (D). Information includes data from this study and data gathered from the literature. Data of this study and Goynes et al. (1993) are for barley and the remaining information is for wheat. The unpublished data are for spring wheat cv. Hank and winter wheat cv. Falcon. The arrow indicates an outlier excluded from the regression (see text for explanation); if included the regression is $e = 1.79 - 0.47D$ ($r^2 = 0.50$, $n = 23$).

conductance with increasing D was similar for two C_4 and two C_3 grasses, but the slope of the decrease in internal leaf CO_2 concentration in response to D was higher in the C_4 species. Zhang and Nobel (1996) found similar results working with different species than Morison and Gifford (1983). Hence, it can be expected that the decrease in leaf photosynthetic rate with increasing D be higher for the C_3 species, as suggested for our comparison of e values for C_3 and C_4 species. However, Bunce (2003) showed that in the range of D from 1.0 to 2.5 kPa, leaf photosynthetic rate decreased by about 60% for both sorghum (C_4) and potatoes (C_3) (Fig. 2 of Bunce, 2003). Therefore, the assertion that the e or the photosynthetic rate of C_4 species is inherently less sensitive to D than the C_3 species remains debatable and needs further study.

CONCLUSIONS

The effects of f_i and plant density on e of barley were insignificant. The maximum e of spring barley estimated in this experiment was 1.19 g MJ^{-1} . This value is below the maximum e of approximately 1.5 to 1.6 g MJ^{-1} reported in the literature (Fig. 5). We assert this is due to greater evaporative demand of the environment in which we measured e . Data in Fig. 5 show that both wheat and barley have similar e , and that the maximum attainable e approaches 1.6 g MJ^{-1} (approximately 2.8 or 3.0 g MJ^{-1} on the basis of intercepted or absorbed PAR, respectively).

There is a strong association between daytime D and e of barley and wheat; the higher D the lower e . Data from the literature suggest that the mechanism involved is a decrease in the photosynthetic rate with increasing atmospheric demand due to an increase in the stomatal resistance, and that this response is a particular case of a general response of the stomata to the transpiration rate. In practical terms, the relation between e and D shown in Fig. 5 can be a useful tool to adjust the e to be used, for example, in crop simulation models.

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